CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE GENETICS

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

NUMBER 15 JULY, 1941

VARIATION OF THE DEER-MOUSE (*PEROMYSCUS MANICULATUS*) ON THE SAND HILLS OF NEBRASKA AND ADJACENT AREAS

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INTRODUCTION

THE extensive sand hills which cover a large part of western Nebraska (Pool, 1914) are inhabited by a race of deer-mouse (*Peromyscus maniculatus nebrascensis*) that is mostly limited to this area of sand (Ostenson, MS). The sand-hill race is much paler and more buffy in pelage color than is the race (*P. m. bairdii*) that inhabits the prairies to the eastward. The more arid plains to the westward of the sand hills are inhabited by a third race (*P. m. osgoodi*) that is larger in some dimensions and is somewhat darker in pelage color than the sand-hill race.

The sand hills are, in many places, sharply marked off from the surrounding more compact soils. These harder surrounding soils often are of a darker color than is the sand. It has accordingly seemed desirable to determine how closely the sand-hill race of deer-mouse is limited to the sand hills and to secure information about the type of intergradation which connects the several races living in the area.

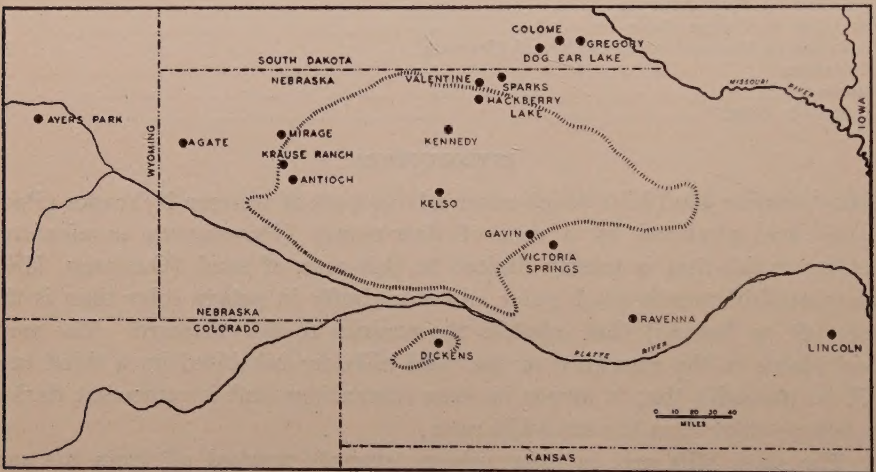
ACKNOWLEDGMENTS

The expeditions on which the breeding stocks of mice for this study were collected were supported by the Carnegie Institution of Washington and by the Museum of Zoology of the University of Michigan. The stocks were collected by Burton T. Ostenson, Palmer R. Sime, Harold J. Leraas, and me. The descriptions of the collecting stations have been supplied by Burton T. Ostenson. The animals were reared and cared for, and the study completed by the Laboratory of Vertebrate Genetics.

METHODS

All the mice herein described were born in the laboratory. After being reared under standard conditions to an approximate age of one year they were killed by ether and were prepared as specimens. The color analysis of the dry, flat skins was made with an Ives tint photometer (Dice, 1932: 5–7, 19–22).

The body measurements of all the mice here described were taken by myself. By mistake, the body measurements of certain individuals of two stocks were made by another member of the Laboratory staff, but these measurements have been omitted in the computation of the means. As a result, the number of individuals used in calculating the means of the external measurements for the Dog-ear Lake stock is 82 and of the Gavin stock is only 36. The measurements of the femurs and skulls and the tint photometer readings were taken by various assistants. The statistical calculations were mostly made by B. J. Bujak.



MAP 1. Map of parts of Nebraska and adjacent states, showing localities at which breeding stocks of mice were collected.

Statistical comparisons between the stocks have been made by the method of Dice and Leraas (1936). Any difference between two means that is greater than about 2.7 times its standard error is considered to be significant.

COLLECTING STATIONS

The stocks of deer-mice here described were secured at the following stations:

Agate. Along the rock ledges on both sides of the Niobrara River, one-fourth of a mile to one mile east of Agate, Sioux County, Nebraska.

Antioch. In sand hills four to seven miles north of Antioch, Sheridan County, Nebraska.

Ayers Park. Along La Prele Creek, one-half mile south of Ayers Park and fifteen miles west of Douglas, Converse County, Wyoming.

Colome. On clay-loam soil five miles southeast of Colome, Tripp County, South Dakota.

Dickens. In a sandy area six miles east and one mile north of Dickens, Lincoln County, Nebraska.

Dog-ear Lake. In a sandy area one-fourth mile north of Dog-ear Lake and fifteen miles southwest of Colome, Tripp County, South Dakota.

Gavin. In sand hills four miles northwest of the railroad siding of Gavin and nine miles northwest of Anselmo, in Custer County, Nebraska.

Gregory. Along the railroad right of way near Gregory, Gregory County, South Dakota.

Kelso. In sand hills near Kelso Park, six miles east of Mullen, Hooker County, Nebraska.

Hackberry Lake. In sand hills around Hackberry Lake, twenty-five miles south of Valentine, in Cherry County, Nebraska.

Kennedy. In sand hills near the ranch-house post office of Kennedy, forty miles south of Valentine, Cherry County, Nebraska.

Krause Ranch. In sand hills on Krause's Ranch, thirty-one miles south of Hay Springs, Sheridan County, Nebraska.

Lincoln. On loamy soil nine miles north of Lincoln, Lancaster County, Nebraska.

Mirage. Along both sides of the Niobrara River in Mirage Township, fourteen miles south of Hay Springs, Sheridan County, Nebraska.

Ravenna. On sandy loam one to two miles east of Ravenna, Buffalo County, Nebraska.

Sparks. In a meadow one and one-half miles west of Sparks, Cherry County, Nebraska.

Valentine. On the grounds of the State Fish Hatchery, in Government Canyon, one mile northeast of Valentine, Cherry County, Nebraska.

Victoria Springs. On loamy soils one-half mile east of the state park at Victoria Springs, which is six miles east of Anselmo, Custer County, Nebraska.

VARIATION IN SOIL COLOR

A sample of the surface soil was collected at each trapping station, was air-dried, and then was brought to the laboratory. The colors of the soil samples have been measured by means of the Ives tint photometer. In making the soil readings the tint photometer is thrown out of focus, so that the general effect of the mass of soil is obtained rather than the color of any particular soil particle.

The several collecting stations have been arranged in Table I in three transects and one isolated station. In each transect the stations first listed are in the Nebraska sand hills and those last listed are outside the sand hills.

In the western transect, Kelso lies near the middle of the sand hills;

TABLE I

Color of Surface Soil in the Sand-hill Region
Mean tint photometer readings of dry soil samples, in per cent

Stations	Red	Green	Blue-violet
Western transect			
Kelso	23.4	18.4	15.5
Antioch	24.0	18.8	14.5
Krause Ranch	23.9	18.7	14.9
Mirage	18.9	15.2	12.0
Agate	24.6	20.3	16.9
Ayers Park	14.1	11.2	9.1
Northeastern transect			
Kennedy	21.6	16.5	13.4
Hackberry Lake	39.3	31.5	25.3
Valentine	26.8	22.7	19.2
Sparks	12.2	9.1	7.4
Dog-ear Lake	14.6	11.4	9.2
Colome	10.1	8.0	6.2
Gregory	no sample	....	....
Southeastern transect			
Gavin	17.7	13.3	10.7
Victoria Springs	14.0	10.6	8.7
Ravenna	15.8	11.6	9.4
Lincoln	no sample	....	....
Isolated sand area			
Dickens	26.8	20.1	15.7

Antioch is in the sand hills, about ten miles from their western border; Krause Ranch is in the sand hills, but only a mile from their western edge; Mirage lies about five miles west of the sand hills; Agate is over fifty miles west of the sand hills; and Ayers Park is one hundred miles west of Agate.

Of the stations in the northeastern transect, Kennedy lies in the main body of the sand hills; Hackberry Lake is about twenty-five miles from the northeastern border of the sand; the Valentine station is just outside the sand hills; Sparks is about seven miles northeast of the sand hills; Dog-ear Lake lies in the middle of an isolated sandy area about thirty miles across; the Colome station is on black clay loam about five miles beyond the sand area surrounding Dog-ear Lake; and Gregory is fifteen miles beyond this sand area.

In the southeastern transect, Gavin lies within the sand hills, but only about five miles from their southeastern edge. Victoria Springs is several miles outside of the sand hills. Ravenna is more than sixty miles southeast of the sand hills. Lincoln lies more than one hundred and seventy miles outside the sand hills.

Dickens lies within a large, isolated sand area south of the South Platte River.

All the stations that are well within the main body of the Nebraska sand hills have soils that are relatively pale, as shown by their high tint photometer readings (Table I). Here are included the Kelso, Antioch, Kennedy, and Hackberry Lake stations. The exceptionally high readings of the Hackberry Lake sample are due to the presence of many soil particles having a high reflectance value. The Krause Ranch and Valentine stations, which lie at the edge of the sand hills, and the Dickens station, from the isolated sand area south of the Platte River, also have soil colors as pale as those of most stations lying within the interior of the sand hills. The soil at the Gavin station, however, from several miles within the sand hills along the southeastern transect, is somewhat darker than the other sand-hill soils. The Agate soil, from more than fifty miles west of the sand hills, has readings as high as many of the sand-hill samples.

The Dog-ear Lake station, although located within a small area of sandy soil, has a shade of soil color considerably below that of the sand hills, but not nearly so dark as that of the Colome station. The Ravenna station likewise is intermediate in soil color, a condition perhaps to be explained by the near-by presence of some small areas of sand. The Victoria Springs station is just southeast of the sand hills, but its soil is considerably darker than that of the sand hills. Mirage lies just west of the sand hills, and its soil is also somewhat darker than that of most of the sand-hill stations. The Ayers Park soil is close in tint photometer readings to the Victoria Springs and Dog-ear Lake soils, being considerably darker than the soil of the sand hills but somewhat paler than the soils from the more eastern prairie areas.

The lowest tint photometer readings, indicating the darkest color of soil for any of the stations in the general sand-hill region are given by the Colome sample. The Sparks soil sample also has relatively low tint photometer readings. No soil samples, unfortunately, are available from the Lincoln and Gregory stations, but it seems probable that the Lincoln station at least would have exhibited still lower readings. The Colome readings correspond fairly closely to those of some prairie stations in eastern North Dakota from which the resident deer-mice are assigned to the subspecies *bairdii* (Dice, 1940: Table I).

In general, then, the sand-hill soils are much paler than the soils of the surrounding areas. Dickens and Agate are the only stations more than a few miles outside the sand hills, the soils of which have as high tint photometer readings as the sand-hill samples. Dickens lies in a large, isolated area of sand, that evidently is very similar in shade of color to the soil of the sand hills. Agate, on the contrary, does not lie in a sandy area, and the reason for the pale color of the soil there is not known to me. It is possible that this sample does not well represent the average of soil color in the vicinity.

The soils of the areas immediately surrounding the sand hills, though they are darker in color than the sand, are distinctly paler than the prairie soils of the eastern parts of Nebraska and the Dakotas. The soil at Ayers Park in Wyoming also is approximately of the same shade as are the soils surrounding the sand hills.

The change in soil color at the border of the sand hills is in general well marked and rather closely correlated with the limits of the sand. One station (Gavin) several miles inside the sand hills, however, has a relatively dark color for its position, and one station (Mirage) a few miles outside the sand hills, has paler soil than most of the other stations around the sand hills.

VARIATION IN PELAGE COLOR

The palest pelage colors among the deer-mice from the sand-hill region are exhibited by the stocks from the midst of the sand. The Hackberry Lake mice have the highest mean tint photometer readings of all the stocks, and the difference between their means and those of the next highest means are statistically significant for reflected green and blue-violet, both from the dorsal stripe and the side, but are not significant for reflected red (Table II).

The Kelso and Krause Ranch stocks rank next in order of paleness, and both these significantly exceed all the other stocks, except the one from Hackberry Lake, in the mean tint photometer readings for the percentage of red reflected from the dorsal stripe and of green and blue-violet reflected from the side of the body. The Kennedy and Antioch stocks, which also were taken on the sand hills, rank fairly high among the stocks, but both are significantly exceeded in tint photometer readings for dorsal-stripe green and blue-violet by the Mirage stock, which comes from just outside the western edge of the sand hills. Although the Gavin stock was secured a few miles inside the southeastern border of the sand hills, it averages darker in pelage color than the other sand-hill stocks, and its photometer readings rank in general with those of the stocks from the immediately surrounding region.

Of the stocks that were secured on the areas adjacent to the sand hills, the Mirage stock ranks highest in tint photometer readings, and for some colors its means exceed, as has already been pointed out, those of certain of the sand-hill stocks. The Victoria Springs stock also ranks fairly high, and for some color comparisons it is not significantly exceeded in mean readings by the Kennedy or Antioch sand-hill stocks. The Dickens stock, which comes from the isolated sand area south of the Platte River, does not differ significantly from the Gavin stock for any color reading, nor are its mean readings significantly less than those of the Kennedy stock for the dorsal stripe, but with these exceptions it has significantly lower mean readings than the sand-hill stocks. The Sparks stock, from the northeastern transect a few miles outside of the sand hills, has mean tint-photometer readings that do not differ significantly from those of the Dickens stock. The stocks from Valentine, which is close to the northeastern edge of the sand hills, and from Ravenna, which lies sixty miles southeast of the sand hills, do not differ significantly from one another in tint-photometer readings, and both

TABLE II

PELAGE COLOR OF *PEROMYSCUS MANICULATUS* FROM THE SAND-HILL REGION
Mean tint photometer readings and standard errors, one-year age class, both sexes, in per cent

Stock	Dorsal Stripe		
	Red	Green	Blue-violet
Western transect			
Kelso	16.94 ± .30	11.13 ± .19	7.54 ± .14
Antioch	13.35 ± .31	9.30 ± .18	6.61 ± .12
Krause Ranch	16.22 ± .37	10.97 ± .23	7.66 ± .15
Mirage	14.67 ± .40	10.25 ± .28	7.33 ± .24
Agate	11.68 ± .20	8.25 ± .14	5.76 ± .12
Ayers Park	11.94 ± .22	8.66 ± .17	6.54 ± .13
Northeastern transect			
Kennedy	14.12 ± .29	9.50 ± .18	6.61 ± .14
Hackberry Lake	17.51 ± .45	12.11 ± .28	8.51 ± .21
Valentine	11.28 ± .18	8.04 ± .12	5.50 ± .10
Sparks	13.82 ± .28	9.09 ± .17	5.92 ± .12
Dog-ear Lake	8.52 ± .19	6.34 ± .15	4.72 ± .11
Colome	8.72 ± .13	6.22 ± .10	4.69 ± .08
Gregory	9.31 ± .18	6.76 ± .13	4.77 ± .09
Southeastern transect			
Gavin	12.59 ± .34	8.77 ± .23	5.82 ± .16
Victoria Springs	14.44 ± .35	9.86 ± .25	7.05 ± .20
Ravenna	11.08 ± .22	7.68 ± .14	5.29 ± .11
Lincoln	6.60 ± .11	5.08 ± .08	3.96 ± .08
Isolated sand area			
Dickens	13.78 ± .30	9.33 ± .21	6.14 ± .15
	Side Stripe		
Western transect			
Kelso	29.52 ± .32	20.03 ± .23	14.37 ± .19
Antioch	25.58 ± .41	18.25 ± .26	13.38 ± .19
Krause Ranch	28.54 ± .46	20.13 ± .30	14.61 ± .22
Mirage	25.83 ± .51	18.02 ± .34	12.83 ± .25
Agate	25.69 ± .32	18.74 ± .27	13.49 ± .23
Ayers Park	24.06 ± .36	17.57 ± .21	13.10 ± .20
Northeastern transect			
Kennedy	28.06 ± .32	18.61 ± .21	12.90 ± .21
Hackberry Lake	29.55 ± .53	21.45 ± .33	15.90 ± .28
Valentine	22.29 ± .32	15.92 ± .23	11.46 ± .18
Sparks	25.19 ± .33	16.68 ± .20	11.30 ± .15
Dog-ear Lake	17.56 ± .18	13.11 ± .14	9.91 ± .13
Colome	18.98 ± .22	13.52 ± .15	9.82 ± .12
Gregory	18.68 ± .24	13.38 ± .17	9.71 ± .14
Southeastern transect			
Gavin	24.05 ± .34	16.30 ± .21	11.19 ± .21
Victoria Springs	25.32 ± .31	17.76 ± .26	12.75 ± .23
Ravenna	21.64 ± .36	15.18 ± .22	10.90 ± .19
Lincoln	15.71 ± .22	11.46 ± .17	8.78 ± .14
Isolated sand area			
Dickens	24.83 ± .45	16.33 ± .29	11.32 ± .24

of these stocks have somewhat lower mean photometer readings than those of the stations closer to the sand hills.

The Agate and Ayers Park stocks, which were both secured many miles west of the sand hills, do not differ significantly from one another in mean readings for some colors, but the Ayers Park readings average significantly the higher in the amount of blue-violet reflected from the dorsal stripe, and the Agate readings average significantly the higher in red and green reflected from the side of the body. These stocks rank in general near the Gavin stock in readings for the dorsal stripe and near the Victoria Springs stock in readings for the side. They are therefore darker than most of the sand-hill stocks, and are of about the same shade as the stocks from the area immediately surrounding the sand hills.

The darkest pelage colors are shown by the easternmost stocks—those from Gregory, Colome, Dog-ear Lake, and Lincoln. The Lincoln stock is the darkest of all and has significantly lower means for all color comparisons than any other of these stocks. The only significant difference between the other three stocks is that the Dog-ear Lake stock has a significantly lower mean for side red than either the Gregory or Colome stocks. All three of these stocks, however, have significantly lower mean readings for all color comparisons than any of the other stocks here described, except the one from Lincoln.

A tendency for pelage color to be correlated with the soil color of the habitat is strongly marked in these mice, as in most other small mammals (Dice and Blossom, 1937: 92–108). Thus, the mice living on the pale-colored sands of the Nebraska sand hills are in general the palest of our stocks. Likewise, the mice living on the darker soils of the eastern prairies are relatively dark in coat color. There are, however, many exceptions to the general trend toward correlation between pelage color and surface-soil color. The Agate and Ayers Park mice, for instance, average nearly the same in tint-photometer readings of coat color, but the soil of the Ayers Park locality has considerably lower readings than the Agate soil. Likewise, the Sparks soil is relatively dark, but the mean color readings for the Sparks mice rank relatively high among the stocks.

The failure of some of the stocks to follow the general trend toward a correlation between their pelage color and the soil color of their habitat is probably due in large part to the occurrence here, as elsewhere, of numerous local races, the characters of which are only partially controlled by the environment (see Dice, 1940*a*: 12–13).

The change from pale-colored, sand-hill deer-mice to the darker-colored deer-mice of the surrounding area occurs fairly close to the border of the sand hills. The number of stations from which mice were collected, however, is not sufficient to establish the precise width of the area of intergradation along each of the transects. For the western transect the Mirage stock, which was taken about five miles west of the sand hills, averages as pale in pelage color as many of the typical sand-hill stocks. The Agate and Ayers Park stocks, however, which were secured many miles to the westward, average decidedly darker in pelage color than the sand-hill mice.

The evidence from the northeastern transect is somewhat confusing. The Valentine stock, which was taken on pale-colored soil just outside the sand hills, averages fairly dark in pelage color, whereas the Sparks stock, which was secured on decidedly dark-colored soil several miles farther away, averages in tint-photometer readings only slightly below some of the stocks from the middle of the sand hills. All the stocks of this transect that were secured at points farther removed than Sparks from the sand hills, average distinctly dark in pelage color.

Along the southeastern transect, the Gavin stock, from several miles inside the sand hills, averages slightly darker in pelage color than the Victoria Springs stock, which was taken several miles southeast of the sand hills. The Ravenna and Lincoln stocks, which were secured many miles southeast of the sand hills, are both much darker in pelage color than the sand-hill mice.

The distance beyond the sand hills to which the pale color characteristic of the sand-hill deer-mice spreads is difficult to determine from the data at hand. It has already been shown that the populations immediately surrounding the sand hills are in general darker in color than those living on the sand. The stocks from farthest west along the western transect differ little in shade of color from those living near the edge of the sand hills. The northeastern and southeastern transects are both broken by local areas of sandy soils, and these paler-colored soils undoubtedly disturb the color gradients along these transects. It is certain that intergrading populations surround the sand hills for about ten or more miles on every side, and that populations fairly pale in pelage color recur on some isolated sand areas, such as on the one at Dickens.

There is much variability of the pelage color in some of these stocks of mice, particularly in those from the stations on the sand hills. Within the stock from Hackberry Lake, for instance, some mice are a rich yellow buff, others are pale buff, and still others are gray. The degree of variability in pelage color of the several stocks is best measured by the standard deviations of the tint-photometer readings. These are given, for reflected red only, in Table III. The standard deviations for the other colors are of approximately the same comparative order as those for red.

The lowest standard deviations for the tint-photometer readings of our stocks, indicating the most uniform pelage colors, are given by the mice from Lincoln, Colome, Dog-ear Lake, and Gregory. Somewhat higher standard deviations, expecially for the readings of the side of the body, are exhibited by the stocks from Agate, Ayers Park, and Ravenna. These seven stations are all located at some distance from the sand hills. In addition, the Valentine stock, from just north of the sand hills, has standard deviations which do not differ significantly from those of the Agate, Ayers Park, or Ravenna mice.

The highest standard deviations are shown by the Krause Ranch and Hackberry Lake stocks, both from stations within the sand hills. The Kelso, Antioch, Kennedy, and Gavin sand-hill stocks are only somewhat less variable. The Mirage stock, from just outside the western edge of the sand hills, is greatly variable, and its standard deviations of color readings fall between those of some of the sand-hill stocks. The Victoria Springs stock, from just southeast of the sand hills, and the Sparks stock, from a few miles northeast of the sand hills, are also considerably variable, and the standard deviations of their color readings for red are not significantly smaller than those of some of the sand-hill stocks. The Dickens stock, from the isolated sand area south of the Platte River, has standard deviations which do not differ significantly from those of the less variable of the sand-hill stocks.

This analysis of the variability of pelage color in these deer-mice shows that none of the populations living on or immediately adjacent to the sand hills are nearly as uniform in color as are the populations of the same species living many miles removed from the influence of the sand.

It might be expected that the populations living in the middle of the sand hills should be more uniform in color than those at the edges, where intergradation with the surrounding races is taking place. However, the sand

TABLE III

Variability of Pelage Color in Deer-Mice from the Sand-hill Region
Standard deviations and standard errors of tint photometer readings, reflected red only, in per cent

Stock	Dorsal Stripe	Side
Western transect		
Kelso	2.98 ± .20	3.37 ± .23
Antioch	2.97 ± .22	3.91 ± .29
Krause Ranch	4.13 ± .26	5.19 ± .33
Mirage	3.64 ± .28	4.61 ± .36
Agate	1.96 ± .14	3.10 ± .22
Ayers Park	1.88 ± .16	2.99 ± .25
Northeastern transect		
Kennedy	2.98 ± .20	3.37 ± .23
Hackberry Lake	4.28 ± .32	5.00 ± .38
Valentine	1.72 ± .13	3.09 ± .23
Sparks	2.82 ± .20	3.25 ± .23
Dog-ear Lake	1.92 ± .13	1.85 ± .13
Colome	1.24 ± .09	2.09 ± .15
Gregory	1.73 ± .12	2.36 ± .17
Southeastern transect		
Gavin	2.94 ± .24	2.88 ± .24
Victoria Springs	3.25 ± .25	2.92 ± .22
Ravenna	1.91 ± .16	3.07 ± .25
Lincoln	1.05 ± .08	2.13 ± .15
Isolated sand area		
Dickens	2.53 ± .22	3.71 ± .32

hills seem to cover too small an area for the establishment there of a uniform race. Some of the stocks from the middle of the sand hills, notably those from Kennedy and from Kelso, do have somewhat lower standard deviations of the tint-photometer readings than some of the stocks, such as Krause Ranch, from near the edge of the hills. On the other hand, the Antioch and Gavin stocks, which were secured within about ten miles of the edge of the hills, are not more variable than stocks from the interior of the sand area.

The considerable variability in pelage color of the sand-hill deer-mice is undoubtedly due in part to the occurrence, nearly throughout the area, of buff and gray color phases, which Clark (1938: 6) has shown to be alternative in inheritance. The buff phase is characteristic of the subspecies *nebrascensis,* whereas the gray phase is in general characteristic of *bairdii.* The determination of the distribution of hereditary color characters in these populations, however, must await a more intensive genetic study, which is now in progress.

VARIATION IN DIMENSIONS OF BODY AND SKELETON

There is a general tendency in most of their dimensions for these deer-mice to be relatively small in the eastern parts of Nebraska and South Dakota and to increase in size toward the west. This is very evident in Table IV, where the stocks have been arranged according to their longitudinal position from east to west.

In making the size comparisons, any stock whose mean for a particular measurement does not significantly exceed the smallest mean of the series is called small; if its mean does not differ significantly from the largest mean, it is called large; and if its mean be both significantly smaller than some mean and significantly larger than some other mean it is ranked as intermediate.

The Lincoln stock, which comes from the easternmost locality, is significantly smaller in hind-foot length than any other of our stocks; it ranks small in tail length, ear length, femur length, mandibular length, condylopremaxillary skull length, and condylozygomatic distance; and it is intermediate in body length and in bullar width of skull.

The Ravenna stock ranks small in ear length, femur length, mandibular length, and bullar width, and is intermediate in all the other measurements.

The Gregory stock ranks intermediate in all measurements. In mandibular length, however, it is fairly large, being significantly exceeded only by the Ayers Park stock.

The Colome stock is intermediate in all its measurements, but in body length only the Valentine stock is significantly shorter and in condylozygomatic distance only the Dog-ear Lake stock is significantly smaller.

The Victoria Springs stock ranks large in femur length and intermediate in all other measurements. In body length, however, only the Valentine stock is significantly smaller, and in tail length only the Dickens stock is significantly larger.

TABLE IV

MEASUREMENTS OF *PEROMYSCUS MANICULATUS* FROM THE SAND-HILL REGION, ARRANGED IN ORDER FROM EAST TO WEST
Means and standard errors of one-year age class, both sexes, in millimeters

Stock	No.	Mean Age in Weeks	No. of Parents	Body Length	Tail Length	Hind-foot Length	Ear Length
Lincoln	95	51	5	93.87 ± .48	54.66 ± .42	18.247 ± .061	14.951 ± .057
Ravenna	73	48	7	94.16 ± .71	60.05 ± .54	19.409 ± .083	14.919 ± .071
Gregory	96	47	14	94.05 ± .46	60.33 ± .42	19.393 ± .077	15.354 ± .095
Colome	94	53	13	92.54 ± .47	58.22 ± .42	19.813 ± .070	15.479 ± .070
Victoria Springs	89	45	9	92.25 ± .40	63.12 ± .43	20.030 ± .056	15.261 ± .061
Dog-ear Lake	102	56	8	93.83 ± .49	58.85 ± .35	19.095 ± .046	15.794 ± .076
Gavin	73	48	6	92.69 ± .71	53.81 ± .68	19.174 ± .102	14.769 ± .096
Sparks	99	53	9	92.57 ± .52	62.97 ± .46	19.678 ± .062	15.078 ± .058
Valentine	92	48	14	90.24 ± .44	59.01 ± .40	19.532 ± .052	15.703 ± .073
Hackberry Lake	91	55	16	92.69 ± .51	60.67 ± .49	20.030 ± .072	15.537 ± .069
Kennedy	109	55	6	95.02 ± .43	56.19 ± .35	19.598 ± .062	15.838 ± .069
Dickens	72	55	7	94.64 ± .50	65.37 ± .51	20.103 ± .063	15.576 ± .087
Kelso	115	49	15	92.43 ± .43	60.99 ± .43	19.506 ± .069	15.441 ± .058
Antioch	89	55	7	95.47 ± .44	60.92 ± .45	19.617 ± .061	16.060 ± .069
Krause Ranch	128	55	21	94.56 ± .40	63.31 ± .45	20.097 ± .081	16.311 ± .059
Mirage	83	55	7	96.96 ± .48	60.88 ± .38	19.992 ± .085	16.401 ± .068
Agate	98	55	9	98.09 ± .39	63.90 ± .42	20.496 ± .060	17.261 ± .074
Ayers Park	70	51	10	98.51 ± .46	63.76 ± .38	20.329 ± .076	17.451 ± .082

TABLE IV—(*Cont.*)

Stock	Femur	Mandible	Condyle-premaxilla	Condyle-zygoma	Bullar Width
Lincoln	15.576 ± .065	15.772 ± .039	23.316 ± .056	16.960 ± .048	10.723 ± .028
Ravenna	15.521 ± .091	15.722 ± .056	23.660 ± .082	17.168 ± .058	10.662 ± .042
Gregory	16.084 ± .070	16.084 ± .057	23.956 ± .074	17.270 ± .053	10.804 ± .033
Colome	15.584 ± .066	15.961 ± .042	23.661 ± .071	17.065 ± .048	10.688 ± .023
Victoria Springs	16.327 ± .084	15.925 ± .045	23.752 ± .059	17.140 ± .038	10.803 ± .021
Dog-ear Lake	15.856 ± .062	15.767 ± .034	23.292 ± .045	16.884 ± .036	10.550 ± .021
Gavin	15.543 ± .084	15.834 ± .053	23.508 ± .076	17.063 ± .051	10.660 ± .025
Sparks	15.697 ± .081	15.871 ± .050	23.789 ± .065	17.136 ± .048	10.730 ± .027
Valentine	15.365 ± .070	15.815 ± .044	23.493 ± .063	16.981 ± .048	10.619 ± .028
Hackberry Lake	15.798 ± .070	16.031 ± .056	24.009 ± .082	17.345 ± .056	10.667 ± .028
Kennedy	15.603 ± .073	16.017 ± .036	24.056 ± .053	17.338 ± .040	10.815 ± .025
Dickens	15.900 ± .079	15.957 ± .050	23.968 ± .054	17.361 ± .041	10.815 ± .028
Kelso	15.529 ± .067	15.660 ± .042	23.798 ± .061	17.234 ± .041	10.690 ± .023
Antioch	16.283 ± .069	15.901 ± .040	24.156 ± .065	17.475 ± .045	10.927 ± .025
Krause Ranch	15.497 ± .050	15.842 ± .032	23.864 ± .047	17.265 ± .038	10.907 ± .028
Mirage	15.859 ± .065	15.999 ± .052	24.227 ± .059	17.455 ± .043	10.682 ± .024
Agate	16.171 ± .069	16.292 ± .053	24.666 ± .075	17.752 ± .054	11.104 ± .025
Ayers Park	16.484 ± .073	16.296 ± .049	24.570 ± .061	17.416 ± .042	10.863 ± .031

The Dog-ear Lake mice are small in mandibular length, condylopremaxillary skull length, condylozygomatic distance, and in bullar width. Only the Lincoln stock has a significantly smaller hind foot. In the other measurements the Dog-ear Lake mice are intermediate.

The Gavin stock ranks small in tail length, ear length, femur length, mandibular length, and skull length. In body length, however, only the Valentine stock is significantly shorter; in hind-foot length only the Lincoln stock is significantly smaller; and in condylozygomatic distance and bullar width of skull only the Dog-ear Lake mice are significantly smaller.

The Sparks stock ranks intermediate in all measurements, though in tail length only the Dickens stock is significantly longer, and in several of the other measurements only a single stock is significantly smaller.

The Valentine stock is significantly shorter in body length than any other stock. It ranks small in femur length, mandibular length, skull length, condylozygomatic distance, and bullar width. In tail length, foot length, and ear length it is intermediate.

The Hackberry Lake mice are intermediate in all measurements, but only the Dog-ear Lake mice average significantly smaller in bullar width of skull.

The Kennedy stock also ranks intermediate among the stocks in all dimensions of the body and skeleton. In tail length, however, only the Gavin stock averages significantly shorter.

The Dickens stock ranks large in length of tail and only the Agate stock significantly exceeds it in length of hind foot and in condylozygomatic distance. In all the other measurements it ranks intermediate.

The Kelso mice rank small in length of femur and length of mandible. In body length only the Valentine mice are significantly smaller, and only the Dog-ear Lake mice average significantly smaller in bullar width of skull. In all other measurements the Kelso mice rank intermediate.

The Antioch stock ranks large in length of femur. In condylozygomatic distance and bullar width of skull it is significantly exceeded only by the Agate stock. On the other hand, only the Kelso stock has a significantly smaller mandible. In all other measurements the Antioch stock ranks intermediate.

The Krause Ranch mice average small in length of femur. In the other measurements the Krause Ranch mice rank intermediate. In length of mandible, however, only the Kelso mice average significantly smaller, and in tail length only the Dickens mice and in hind-foot length only the Agate mice average significantly larger.

The Mirage stock ranks intermediate in all measurements. In body length, however, it is significantly exceeded only by the Ayers Park stock and in condylozygomatic distance only by the Agate stock. In bullar width of skull only the Dog-ear Lake stock is significantly smaller.

The Agate stock averages significantly larger than any other stock in condylozygomatic distance and in bullar width of skull. Furthermore, it averages large also in body length, hind-foot length, tail length, ear length, length of mandible, and skull length. In femur length it is significantly exceeded only by the Ayers Park stock.

The Ayers Park mice average large in body length, tail length, hind-foot length, ear length, femur length, length of mandible, and condylopremaxillary skull length. In condylozygomatic distance and bullar width of skull the Ayers Park mice are significantly exceeded only by the Agate mice.

It will be noted that the Lincoln and Ravenna stocks, which are from the two most easterly localities here described, are the smallest in nearly all dimensions of the body and skeleton. Likewise, the Agate and Ayers Park stocks, from the most westerly localities, rank large in all measurements. The remaining stocks, including all those from the Nebraska sand hills, are more or less intermediate in measurements, as they are in geographical position, between the eastern and western extremes.

The gradation in measurements from east to west is not uniform in these stocks, but, on the contrary, is decidedly irregular, indicating the existence of many local populations differing from one another in size characters. There is, nevertheless, a fairly consistent trend, so that the mice from the eastern edge of the sand hills tend in general to be somewhat smaller in most dimensions than those from the western edge of the sand. For instance, in ear length the stocks from the sand hills and the immediately adjacent stations fall into the following order of magnitude of means, beginning with the smallest: Gavin, Victoria Springs, Kelso, Hackberry Lake, Valentine, Kennedy, Antioch, Krause Ranch, and Mirage. This order follows longitude closely. Some of the other measurements do not show as consistent an east-west trend as ear length. Nevertheless, the tendency toward increase in size to the westward is evident in all the measurements.

DISCUSSION

A conspicuous geographical gradient ("cline" of Huxley, 1939) is produced in the sand-hill region by the tendency for the pelage color of the deer-mice to be correlated with the soil color of their habitat. The deer-mouse population on the pale-colored sand of the Nebraska sand hills is accordingly predominantly pale in pelage color. Around the sand hills on every side both the soil and the mice tend to be darker. On isolated sandy areas, however, such as on the one at Dickens, and on other areas with pale soils, there are local, pale-colored populations.

Another important geographical trend in the sand-hill area is the trend toward smaller dimensions of body and skeleton on the eastern prairies and larger dimensions in the west. The resultant size gradient is wholly independent of the gradient of pelage color. Indeed, the size gradient continues across the sand hills, just as though they were not there. In conformance with this gradient, the deer-mice from the eastern parts of the sand hills in general average slightly smaller than those from the western parts.

The east-west gradient in dimensions that is evident in the deer-mice of the sand-hill region also is present in the mice of the same species in North Dakota (Dice, 1940*a*: 6–8). This geographical size gradient seems, therefore, to be characteristic of the deer-mice of all the northern part of the Great Plains.

The pale pelage color of the sand-hill deer-mice is definitely correlated with the pale-colored sandy soil of their habitat. This correlation is, therefore, an ecologic one. On the other hand, it is not known whether or not the trend toward increase in size of the mice westward across the Great Plains is correlated with any particular environmental feature. It is possible that this geographic size gradient also has an ecological basis, but that has not been demonstrated.

Many local deer-mouse populations in this region fail to conform to the expected geographic gradients of size and color. A similar sort of local variation has been shown to occur in other regions. In part, the characters of the local color races may be correlated with local variations in soil color. To a considerable degree, however, these local populations seem to be independent of ecological factors, and many of them may be produced by chance combinations of genes (Dice, 1940*b* : 212–13).

The type of geographic intergradation exhibited by pelage color in this region contrasts markedly with that of size characters. Size characters in these mice tend to intergrade rather evenly. This perhaps is correlated with the general rule that in mammals size is inherited in a more or less blending manner. In pelage color, on the contrary, many of the populations from the sand hills and the surrounding areas are highly variable, and some individual mice may be indistinguishable from individuals of the darker-colored adjacent subspecies. The inheritance of the color characters buff and gray in an alternative manner undoubtedly is in part responsible for this considerable variability of pelage color within the sand-hill populations.

The hereditary factors which are responsible for the pale colors of the sand-hill mice and of the pale-colored isolated populations which appear elsewhere on the Great Plains have not yet been determined. It is known, however, that the buff and gray alternative factors, which in part distinguish the subspecies *nebrascensis* from *bairdii,* are widespread in deer-mouse populations (Clark, 1938: 6). It is probable that many other inherited color factors are also widely distributed. The origin of a local color race is therefore probably not usually dependent upon the occurrence at that place of a new mutation, but rather, in most cases, results from the preponderance there of a particular combination of widely distributed genes.

The stock of deer-mice from Lincoln, Nebraska, which is our easternmost locality, is here assigned to the subspecies *Peromyscus maniculatus bairdii.* This form is dark in pelage color and small in most of the dimensions of its body and skeleton (Osgood, 1909: 79). There is, however, a considerable amount of variation in pelage color and in dimensions from place to place within the range of the subspecies (Dice, 1937: Tables I and II). The pale-colored deer-mice from the Nebraka sand hills are placed in the subspecies *nebrascensis* (*luteus* of Osgood, 1909: 77–78). This form is moderately small in body dimensions, and pale in pelage color. The stocks from Ayers Park and Agate are assumed to be of the subspecies *osgoodi* (*nebrascensis* of Osgood, 1909: 75–76), which is said to be of a pale color, but larger in certain body and skeletal dimensions than *nebrascensis* or *bairdii.*

The recognition of the three subspecies *bairdii, nebrascensis,* and *osgoodi* calls attention to geographical trends in deer-mouse characters which are important. In a broad view of the geographical distribution of the species, these subspecies accordingly are useful units of classification, but when we attempt to draw the boundaries between these geographical races in the sand-hill region we encounter considerable difficulty. Some of the stocks here described can definitely be assigned, on the basis of their average characters, to one or another of the three above-mentioned subspecies, but many of the stocks exhibit intermediate characters and, according to the usual practice of mammalogists, must be considered to be intergrades. Unfortunately, however, the characters of body size do not intergrade in this region at the same places nor in the same manner as do the characters of pelage color. The result is that nearly all the stocks in this region are intergrades either in size or color or in both characters.

Little would be gained if we should attempt to assign each of these stocks of deer-mice or each individual specimen to a particular subspecies. On the contrary, it seems better to consider the subspecies here to represent geographic trends that at some localities are clearly expressed, but which in many intermediate areas are confused by the occurrence of local conditions and local races.

From the ecological point of view, the subspecies *nebrascensis* represents a tendency for the evolution of a pale-colored population of deer-mice on the pale-colored sand of the Nebraska sand hills. This tendency, however, is opposed by constant interbreeding with darker-colored races around the borders of the sand hills. The sand hills seem not to cover a sufficient area, or perhaps selection is not sufficiently rigorous there, to have produced a uniformly pale race. On the contrary, most of the sand-hill populations are highly variable in color, and even in the midst of the main area of sand a small proportion of the deer-mice are dark in pelage color.

The incipient pale-colored populations on the smaller, isolated areas of pale-colored sand elsewhere on the Great Plains are still more subject to swamping by the surrounding darker-colored races than are those in the sand hills. This is probably the reason why the Dickens stock averages somewhat darker in pelage color than most of the sand-hill stocks. Nevertheless, the same parallel tendency for the evolution of a pale-colored race may be assumed to be present on this isolated sand area as on the larger area of sand hills.

SUMMARY

The tendency of the pelage color of deer-mice to be correlated with the soil color of the local habitat has resulted in the development of a pale-colored geographical race, *Peromyscus maniculatus nebrascensis,* on the pale-colored soils of the Nebraska sand hills. The sand-hill race, however, is nowhere uniform in pelage color, and every local population has a high degree of variability in shade of color. This variability is probably due in considerable part to constant interbreeding with the darker-colored populations which surround the sand hills on every side.

The dimensions of the body and skeleton are relatively small in the deer-mice living on the prairies of eastern Nebraska and eastern South Dakota (subspecies *bairdii*), whereas the mice of western Nebraska and eastern Wyoming are larger in size (subspecies *osgoodi*). The resulting geographical gradient of deer-mouse size passes without interruption across the sand hills. The geographical gradients of pelage color and of body dimensions are therefore independent of one another in the deer-mice of this area.

The geographical gradients of pelage color and of body dimensions seldom proceed evenly, but are frequently broken by the occurrence of local races which do not conform to the general trends. A local race which is moderately pale in pelage color lives on an isolated sandy area around Dickens. This local race does not average so pale in pelage color as the mice living on the larger body of the sand hills. Its evolution is presumed, however, to have been directed, in a nearly parallel manner, by the same ecological forces which produced the sand-hill race.

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